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Sección Especial
IMPACTO DE ACTIVIDADES PRODUCTIVAS SOBRE MAMÍFEROS DE ARGENTINA

FLUCTUATING ASYMMETRY AS AN INDICATOR OF ENVIRONMENTAL STRESS IN SMALL MAMMALS

José A. Coda[1], Juan José Martínez[2], Andrea R. Steinmann[1], José Priotto[1], and Ma. Daniela Gomez[1]

[1] Universidad Nacional de Río Cuarto, Río Cuarto, Argentina. CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Argentina. [Correspondencia: <joseacoda@gmail.com>]
[2] Instituto de Ecorregiones Andinas (INECOA), Universidad Nacional de Jujuy, CONICET, San Salvador de Jujuy, Argentina.

ABSTRACT. The developmental stability of an organism is reflected in its ability to produce an 'ideal' form under a particular set of conditions. Bilateral structures in bilaterally symmetrical organisms offer a precise symmetry against which departures may be compared. The tool mostly used to estimate the development stability is fluctuating asymmetry, which considers small random deviations that occur between the left and right sides of a bilateral trait. Fluctuating asymmetry is considered as the only form of asymmetry that can serve as a useful indicator of environmental/genetic stress. We summarized four decades of studies where fluctuating asymmetry was used to assess the effects of environmental stress in small mammals. This group of species has been widely used in ecological studies to infer environmental disturbances because of its wide range of characteristics. We selected 27 articles that were compiled with Google Scholar (Mountain View, CA) using "fluctuating asymmetry" and "small mammals" as key words, written in English and with ecological objectives. We focused our analyses on the approaches used to evaluate fluctuating asymmetry (linear measurements or geometric morphometrics), the stress factor (natural or anthropogenic), the region where the study was developed, the number of traits used in the studies and the data sources, including measures obtained from samples of barn owl pellets, scientific collections and captured animals. The review shows the importance of including fluctuating asymmetry in ecological studies as a reliable, cheap and fast biological indicator of the effect of environmental stress on mammals.

RESUMEN. Asimetría fluctuante como un indicador de estrés ambiental en pequeños mamíferos. La estabilidad del desarrollo de un organismo se refleja en la capacidad que posee de producir una forma "ideal" bajo un conjunto particular de condiciones. Las estructuras bilaterales en organismos con simetría bilateral ofrecen una simetría precisa sobre la cual se pueden comparar desviaciones. La herramienta más utilizada para estimar la estabilidad del desarrollo es la asimetría fluctuante, la cual considera las pequeñas desviaciones aleatorias que ocurren entre los lados derecho e izquierdo de rasgos bilaterales, y es la única asimetría adecuada como indicador de estrés ambiental/genético. Resumimos cuatro décadas de estudios en donde la asimetría fluctuante fue utilizada para evaluar el efecto de estrés ambiental sobre pequeños mamíferos. Este grupo de especies ha sido ampliamente utilizado en estudios ecológicos para inferir perturbaciones ambientales debido a sus variadas características. Se seleccionaron 27 artículos compilados con Google Académico, utilizando "asimetría fluctuante" y "pequeños mamíferos" como palabras claves, escritas en inglés y con objetivos ecológicos. Centramos nuestro análisis en los enfoques utilizados para evaluar la asimetría fluctuante (medidas lineales o morfometría geomé-

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trica), el factor de estrés (natural o antropogénico), la región donde se desarrolló el estudio, el número de rasgos utilizado en los estudios y las fuentes de datos (muestras de pellets de lechuza, colecciones científicas y capturas directa de animales). La revisión muestra la importancia de incluir la asimetría fluctuante en estudios ecológicos como un indicador biológico confiable, económico y rápido del efecto del estrés ambiental sobre los mamíferos.

Key words: Developmental stability. Geometric morphometrics. Linear measurements. Rodents. Shrews.

Palabras clave: Estabilidad del desarrollo. Medidas lineales. Morfometría geométrica. Musarañas. Roedores.

INTRODUCTION

Environmental stress can have significant detrimental effects on animal populations (Lazić et al. 2013, 2015). Several authors have proposed that obtaining a sensitive indicator of stress is crucial for conservation biologists, since it can be used to detect signs of population disturbance before components of fitness have been affected and irreversible demographic damages have occurred (Leary & Allendorf, 1989; Teixeira et al., 2006; Delgado-Acevedo & Restrepo, 2008; Beasley et al., 2013; Lazić et al., 2013). Traditional biomarkers (molecular and cellular exams, heat shock proteins, hemoglobin adducts, etc.) may be reliable, but they are expensive and may not be applicable across species (Helle et al. 2011; Lazić et al. 2013). The developmental stability of an organism is reflected in its ability to produce an 'ideal' form under a particular set of conditions. The lower its stability, the greater the likelihood it will depart from this 'ideal' form. Ideal forms are rarely known a priori, but bilateral structures in bilaterally symmetrical organisms offer a precise expectation of symmetry against which departures may be compared. Thus, the study of bilateral traits provides a very convenient method for assessing deviations from the norm and studying the factors that may influence such deviations (Palmer & Strobeck 1986; Palmer 1994). The developmental precision that produces bilaterally symmetric structures may be negatively affected by a wide range of environmental and/or genetic stressors (Zakharov 1992).

Subtle departures from symmetry are most commonly described by frequency distributions of right-left sides of a trait (Palmer 1994). Such frequency distributions usually exhibit one of the following three patterns: directional asymmetry, antisymmetry and fluctuating asymmetry. Directional asymmetry is characterized by a normal distribution that is not centered around zero but is significantly biased towards larger traits either on the right or the left side (**Fig. 1A**). Examples include lateral placement of organs such as the heart and liver in humans and muscle-size asymmetries in birds (Markow 1995). Antisymmetry is distinguished by a platykurtic (broad peaked) or bimodal distribution of right-left differences around a zero mean (Palmer & Strobeck 2003) (**Fig. 1B**). A classic example is the claw size in male fiddler crabs. Fluctuating asymmetry is defined as small and random deviations from perfect bilaterally symmetrical traits (Ludwig 1932; Palmer & Strobeck 1986) (**Fig. 1C**). This asymmetry has normal distribution with zero mean. Of these three asymmetries, fluctuating asymmetry is considered as the only form of asymmetry that can serve as a useful indicator of environmental/genetic stress (Palmer & Strobeck 1986; Leary & Allendorf 1989; Leung & Forbes 1997; Polak & Taylor 2007).

The study of fluctuating asymmetry per se began with the work of a small group of researchers, including Ludwig (1932), Thoday (1953, 1956, 1958), Van Valen (1962), and Soulé (1966, 1967). Early perceptions of the importance of fluctuating asymmetry were summarized by Jackson (1973), who pointed out that the level of fluctuating asymmetry can be considered as a measure of buffering capacity in development, since any non-consistent differences between paired structures could

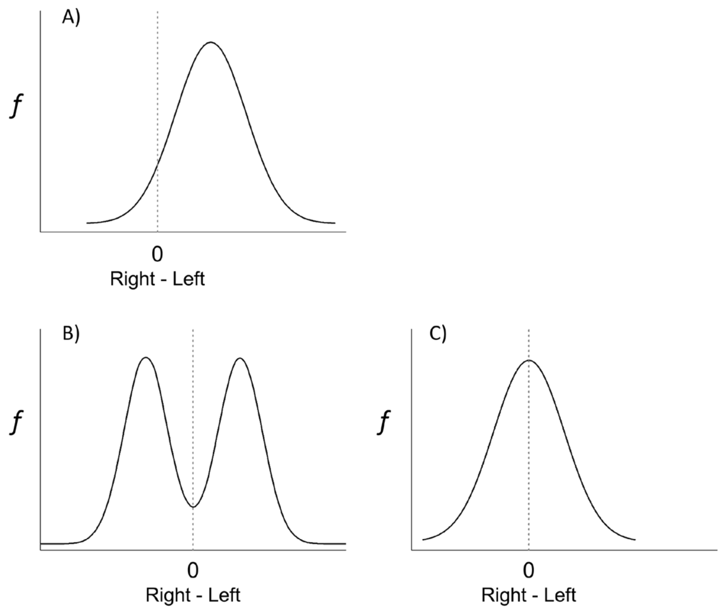

Fig. 1. Three common distributions of right-left in bilateral traits: A) directional asymmetry, B) antisymmetry, C) fluctuating asymmetry. *f*: frequency of the measured trait.

be developmental accidents. The attractiveness of fluctuating asymmetry as a potential biomarker stems from its broad application across biological systems and stressors. An additional advantage is the relative ease in taking trait measurements compared to other biomarkers that require more costly equipment or reagents (Leung et al. 2003). There are two general approaches to study fluctuating asymmetry: geometric morphometrics that provides information about traits morphology using shape and size, and linear measurements that include metrical measurements (lengths) or meristic traits, both on the left and right sides of organisms (Van Valen 1962; Palmer & Strobeck 1986). The geometric morphometrics methodology has been more recently developed and its fundamental advances over traditional approaches (linear measurements) are due to powerful statistical methods designed for the analysis of shape data rather than the use of standard multivariate methods (Rohlf & Corti 2000).

Small mammals have been widely used as model species in ecological studies to infer environmental disturbances because of their wide range of characteristics (Wolff & Sherman 2007). These organisms inhabit all continents except Antarctica and they occur in terrestrial, subterranean, arboreal, and aquatic habitats. They are crucial in their contribution to well-structured food webs (Salamolard et al. 2000; Michel et al. 2006; Baraibar et al. 2009), the consumption and dispersal of plant products (Carey et al. 1999) and mycorrhizal fungi (Maser et al. 1978) and the consumption and control of invertebrates (Elkinton et al. 1996). Most of them are very prolific, have a short life cycle and are relatively easy to capture (Steinmann & Priotto 2011; Korpimaki & Norrdahl 2013). Besides, they constitute a diverse group, with different degrees of habitat specialization, social and mating systems. All these characteristics make this group of mammals a very convenient model for ecological studies.

Currently, there is a challenge to identify vulnerable populations before irreversible demographic/genetic damage takes place. Obtaining of a reliable, general and easy-to-use biomarker of health and wellbeing of individuals that can be applied in ecological studies is therefore important. The aim of this study was to show the relevance of fluctuating asymmetry as a tool to measure environmental stress in ecological studies, with emphasis on small mammals. We summarized four decades of studies where this index was used to assess the effects of environmental disturbances on small mammals.

DATA AND METHODS

Data were compiled with Google Scholar (Mountain View, CA) using two keywords: “fluctuating asymmetry" and "small mammals". We also searched in the reference lists of selected articles additional studies that met our inclusion criteria. We applied other selection criteria to include the papers in this review. Due to the fact that the small mammals are not classified as a taxonomic group we included in this group any species of mammals with adult weights up to 1 kg. We selected only articles in English and with ecological objectives published from 1980 to 2017.

RESULTS AND DISCUSSION

We selected 27 articles (**Table 1**) that met our selection criteria. This small number of articles demonstrates that fluctuating asymmetry is not widely used in ecological studies of small mammal. The highest number of articles in this topic was registered between 2000-2004 (8 articles) and 2015-2017 (5 articles). We found studies carried out in several parts of the world, but most were developed in Europe (20 articles), six in the Americas and only one in Africa. In relation to those studies developed in the Americas, only two were carried out in the Neotropical region (Argentina and Brazil) and the others in United States and Canada (three and one articles respectively). The Neotropical region has suffered major transformations due to land use change and associated negative impacts on biodiversity in the last decades (Ceballos & Garcia 1995; Lowe et al. 2005; Bedano & Domínguez 2016); the lack of fluctuating asymmetry studies in small mammals in this region is remarkable.

Regardless of the approach used to analyze fluctuating asymmetry (linear measurements or geometric morphometrics) the dominant focal species were rodents and shrews. Of the total number of studies, 20 applied linear measurements, six geometric morphometrics and only one used both methodologies. Linear measurement studies used metrical o meristic measures indifferently. The oldest articles applied linear measurements and since 2002 some authors started to use geometric morphometrics. The results obtained from geometric morphometrics and linear measurements were similar with positive association between fluctuating asymmetry and environmental stress in more than 70% of the studies. Thus, both approaches would allow a proper analysis of fluctuating asymmetry in ecological studies of small mammal.

Several authors propose that multiple traits are necessary to test differences in developmental instability in linear measurement analyses (Leary & Allendorf, 1989; Palmer, 1994). Of the total of 21 linear measurement studies, 19 used more than five traits, 15 of which found a positive association between fluctuating asymmetry and environmental stress. On the other hand, Wauters et al. (1996) and Coda et al. (2016) used only one trait and found a positive association between environmental stress and developmental instability. In these studies, the authors used the length of right and left hind feet to assess fluctuating asymmetry in live red squirrels and cricetid rodents. The absence of fluctuating asymmetry could not be accurately established using only one trait.

The environmental stress factors were natural (9 studies) or anthropogenic (18 studies). The natural factors included differences in habitat suitability and only one study analyzed natural disasters (i.e., tornados) (**Table 1**). In relation to anthropogenic factors, most of the studies evaluated the effect of radiation emitted by nuclear power plants and waste from industries/mining (five and eight articles respectively). We registered only two studies about the effect of agriculture on developmental instability in small mammals (**Table 1**), in spite of the fact that agriculture is among the predominant global changes of the last 100 years (Matson et al. 1997) and that it has led to a widespread decline in biodiversity (Benton et al. 2003).

The studies considered used measures obtained from samples of barn owl pellets, scientific collections and animals captured in field surveys that were sacrificed or not. We found only one study in which teeth obtained from barn owl pellets were used to assess fluctuating asymmetry (Amarena et al. 1993). Taking into account the small number of studies about fluctuating asymmetry in small mammals, scientific collections provide a large amount of information for studies of developmental instability (e.g. Sánchez-Chardi et al. 2013; Askay et al. 2014; Maestri et al. 2015). Besides, it is possible to analyze the effects of environmental changes on individual development

Table 1

List of the articles selected to evaluate the use of fluctuating asymmetry as a tool to measure environmental stress in ecological studies on small mammals in chronological order.

Articles authors (Year)	Animals source	Approach (trait)[a]	Stressor	Results[b]	Focal species group	Study area (country)
Pankakoski (1985)	Capture and sacrifice	LM (meristic)	Habitat suitability (natural causes)	+	Rodent	Finland
Owen & McBee (1990)	Capture and sacrifice	LM (metrical)	Industries/Mining	-	Rodent	EEUU
Zakharov et al. (1991)	Capture and sacrifice	LM (metrical and meristic)	Habitat suitability (natural causes)	+	Shrew	Russia, Finland
Amarena et al. (1993)	Barn owls pellets	LM (metrical)	Industries/Mining	+	Rodent and shrew	Italy
Vasil'ev & Vasil'eva (1995)	Capture and sacrifice	LM (meristic)	Radiation	-	Rodent	Russia
Vasil'ev et al. (1996)	Capture and sacrifice	LM (meristic)	Radiation	+	Rodent	Russia
Wauters et al. (1996)	Capture without sacrifice	LM (metrical)	Habitat suitability (human activities)	+	Rodent	Belgium
Zakharov et al. (1997a)	Capture and sacrifice	LM (meristic)	Habitat suitability (natural causes)	+	Shrew	Russia
Zakharov et al. (1997b)	Capture and sacrifice	LM (meristic)	Habitat suitability (natural causes)	-	Shrew	Russia
Badyaevet et al. (2000)	Capture and sacrifice	LM (metrical)	Habitat suitability (human activities)	+	Shrew	EEUU
Nunes et al. (2001)	Capture and sacrifice	LM (metrical)	Industries/Mining	+	Rodent	Portugal
Gileva & Nokhrin (2001)	Capture and sacrifice	LM (metrical)	Radiation	+	Rodent	Russia
Oleksyk et al. (2002)	Capture and sacrifice	GM	Radiation	+	Rodent	Ukraine
Marchand et al. (2003)	Capture and sacrifice	GM and LM (metrical)	Habitat suitability (human activities)	partial	Rodent	France
Knopper & Mineau (2004)	Capture without sacrifice	LM (metrical)	Pesticides	-	Rodent	Canada
Oleksyk et al. (2004)	Capture and sacrifice	GM	Radiation	+	Rodent	Ukraine
Veličković (2004)	Capture and sacrifice	LM (metrical)	Industries/Mining	partial	Rodent	Serbia
Veličkovic (2007)	Capture and sacrifice	LM (meristic)	Industries/Mining	+	Rodent	Serbia

(Table 1 cont.)

Articles authors (Year)	**Animals source**	**Approach (trait)[a]**	**Stressor**	**Results[b]**	**Focal species group**	**Study area (country)**
Wójcik et al. (2007)	Capture and sacrifice	LM (meristic)	Habitat suitability (natural causes)	+	Shrew	Poland
Hopton et al. (2009)	Capture without sacrifice	LM (metrical)	Natural disasters	+	Rodent	EEUU
Sánchez-Chardi et al. (2013)	Specimens from collections	GM	Industries/Mining	+	Shrew	Spain
Askay et al. (2014)	Specimens from collections	GM	Habitat suitability (human activities)	-	Rodent	Africa (5 countries)
Shadrina & Volpert (2014)	Capture and sacrifice	LM (meristic)	Industries/Mining	+	Rodent and shrew	Russia
Maestri et al. (2015)	Specimens from collections	GM	Habitat suitability (natural causes)	+	Rodent	Brazil
Coda et al. (2016)	Capture without sacrifice	LM (metrical)	Habitat suitability (human activities)	+	Rodent	Argentina
Shadrina & Volpert (2016)	Capture and sacrifice	LM (meristic)	Habitat suitability (natural causes)	+	Rodent and shrew	Russia
Yalkovskaya et al. (2016)	Capture and sacrifice	GM	Industries/Mining	+	Rodent	Russia

[a] Approaches to study FA: geometric morphometrics (GM) and linear measurements (LM) that include metrical or meristic measurements.
[b] Positive and negative relationships between FA levels and stressors are indicated with + (plus) and – (minus), respectively.

instability at greater spatial and time scales, which become important in populations that have undergone decreases in their abundances. Museum specimens allow the use of both geometric morphometrics and linear measurements. We found that most studies (19) used sacrificed individuals to take measurements for fluctuating asymmetry analyses, whereas only four used live animals (**Table 1**). Studies based on sacrificed animals used both geometric morphometrics and linear measurements, whereas only linear measurements were used with live animals. Regardless of whether measurements have been obtained from sacrificed or live animals, positive associations between developmental instability and environmental stress was observed in most studies (**Table 1**).

The use of exomorphological traits seem to be a useful tool to assess the relationship between developmental instability and environmental stress, since it can be used with live animals, is easy to obtain and shows similar results to those obtained from measurements of internal traits of sacrificed animals. However, to increase accuracy several measurement of each trait should be taken (repeatability of the measure) and as much traits as possible should be considered.

PERSPECTIVES

Few studies have evaluated the relationship between developmental instability (using fluctuating asymmetry as a proxy) and environmental stress in small mammals. These studies clearly show that fluctuating asymmetry is a tool to assess this relationship, allowing us to suggest that this approach will prove to be increasingly important in future ecological studies.

Fluctuating asymmetry of exomorphological traits may provide a valuable indicator of environmental stress in small mammals. Particularly, the use of non-invasive technique in live wild animals using these traits would be a valuable and inexpensive tool for studies in conservation biology as an alternative to sacrificing animals. To our knowledge, there are no studies that use geometric morphometrics with exomorphological measurements to evaluate fluctuating asymmetry. However, it would be possible to implement this approach with these traits, since they have been already used in studies of leg shape and locomotion in rodents (Rivas & Linares 2006).

This review shows the importance of including fluctuating asymmetry in ecological studies as a reliable, cheap and fast biological indicator of the effect of environmental stress on mammals, especially in the Neotropical region, where there is a noticeable absence of these kinds of studies.

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